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THE POLYCYSTID GREGARINES OF THE UNITED STATES (Third Contribution).

BY HOWARD CRAWLEY.

In 1853 Leidy described a gregarine parasite of the common cricket. To this animal he gave the name of Gregarina achetæ-abbreviatæ, the host being at that time known as Acheta abbreviata. The parasite was illustrated by figs. 32–34 of Leidy's plate 11. In my first communication on our gregarines (Crawley, 1903) I reproduced two of Leidy's figures, and based my description partly upon these and partly upon his text. A glance at these figures, Nos. 34 and 35 of my paper, will suggest at once that they portray different species of gregarines, and studies which I made during the summer of 1906 show that this is so. For the animal shown in Leidy's fig. 34, copied in my fig. 35, I have retained the name given by Leidy, while the other is tentatively placed in the genus Stenophora. I have also considered it advisable to redescribe Gregarina achetæ-abbreviatæ, and have given a new figure, a camera outline from a living solitary gregarine.

Gregarina achetæ-abbreviatæ Leidy. (Pl. XVIII, fig. 1.)

Gregarina achetæ-abbreviatæ Leidy (1853), p. 238, pl. 11, fig. 34. Gregarina achetæ-abbreviatæ Crawley (1903), p. 45, pl. 3, fig. 35. Gregarina achetæ abbreviatæ Crawley (1903a), pp. 639, 641.

Protomerite.—Hemispherical to globular, broader than long. Shape modified in the associations.

Deutomerite.—Ellipsoidal to oval.

Epicyte.—Thin, delicately striated.

Sarcocyte.—Thin, but present all over the animal.

Myocyte.—Easily demonstrated by the use of reagents.

Entocyte.—Dense, but, following the usual rule, less dense in the protomerite than in the deutomerite. In most of the specimens which I encountered, the peripheral part of the entocyte was almost free of granules; this phenomenon being much more conspicuous in the deutomerite than in the protomerite.

Nucleus.—Not seen.

Size.—The largest solitary animal I saw was 500 microns long.

Habit.—Solitary or associated in pairs.

Cysts.—Spherical, provided with a thick gelatinous envelope Diameter of cyst mass, 225–275 microns. Thickness of gelatinous envelope, 30–300 microns. Dehiscence by sporoducts, 2–5 in number, reaching a length of 1,000 microns. Prior to evagination, the situation

of the sporoducts is plainly indicated by the appearance around the periphery of the cyst of dense discoid masses. These are yellowish in color, owing to the presence of oil. Time required for maturation, 1-4 days.

Spores.—Cylindrical, with rounded ends to dolifirm. Dimensions, 4.5 by 2.25 microns.

Host.—Gryllus abbreviatus Serv.

Locality.—Beach Haven, New Jersey, and Wyncote, Pennsylvania.

Stenophora erratica sp. n. (Pl. XVIII, fig. 5.)

Gregarina achetæ abbreviatæ Leidy (1853), p. 238, pl. 11, fig. 33. Gregarina achetæ abbreviatæ Crawley (1903), p. 45, pl. 3, fig. 34.

The general form of this gregarine is shown in fig. 5, which was drawn from a young individual, 150 microns long. In the older animals, while the protomerite is much as here shown, although at times relatively shorter, the deutomerite varies considerably in shape. In some its outline is an elongated ellipse, while in others it is broadest near the posterior end, tapering slowly and gradually forward to the septum. The largest animal seen was 500 microns long.

The epicyte shows distinctly a double contour, and is 1.5 microns thick. The sarcocyte is present all over the animal, and reaches a thickness of 2.5 microns. At the anterior tip of the protomerite, the ectosarc is often thickened to form a low papilla, within which are traces of a pore. It is this character which led me to place the gregarine in the genus *Stenophora*. The entocyte is dense, except in the anterior third of the protomerite, where it is almost free of granules.

These gregarines are not at all polymorphic, but almost constantly display the progressive movement. They are by no means infrequent in crickets, but always present in small numbers. The suggestion is permissible that this form is actually the common *Stenophora julipusilli* Leidy, somewhat altered in appearance from being in the wrong host. Crickets and Julidæ frequently occur in the same environment, and the former might readily swallow spores derived from the feces of the latter. This done, the spores might readily develop, although producing slightly atypical gregarines. There is an excellent field here for experimental work.

In addition to the two forms considered above, the cricket harbors a third, a true *Gregarina*, which is herewith described.

Gregarina kingi¹ sp. n. (Pl. XVIII, figs. 10-12.)

Protomerite.—In the primites, the protomerite, as seen in fig. 10,

¹ To Dr. H. D. King.

is sometimes saddle-shaped. While this peculiarity of contour is not always so striking as here shown, the protomerite is always broad and swollen in front, and much narrower behind. This serves to separate this species from *Gregarina achetæ-abbreviatæ*. In the satellites, the protomerite is subspherical to compressed.

Deutomerite.—Cylindrical, generally somewhat broader in front. Outlines often irregular.

Epicyte.—Very delicate.

Sarcocyte.—Feebly developed, except in the anterior part of the protomerite, where there is a conspicuous crescentic thickening. According to my observations, this character was more marked in the younger than in the older animals.

Entocyte.—Not dense.

Nucleus.—Moderate in size.

Size.—Largest pair seen, 350 microns long.

Habit.—Nearly always associated in pairs. Satellite generally slightly and sometimes considerably smaller than the primite. When the connection between a pair is broken, the anterior surface of the protomerite of the satellite shows a slightly raised ring. Thus the posterior end of the primite fits into a very shallow saucer on the anterior end of the satellite.

Movements.—The gregarines seen were more or less constantly bending and contracting, but showed little or no disposition to progress.

Cysts.—Round, occasionally oval. The cyst mass varies from 90–110 microns in diameter. There is a cuticular wall 6–7 microns thick, outside of which a gelatinous envelope develops. In newly formed cysts, taken from the mid-gut of the host, the gelatinous envelope is so diaphanous as to appear merely as a halo round the dense central mass. But in cysts taken from the feces in the hind-gut, the gelatinous envelope is much more evident. This change in appearance is doubtless merely due to the accumulation of detritus.

Of the cysts found in the host intestine, some are uniformly opaque, with a clear space just inside the cuticle. Others are less opaque, sometimes mottled; sometimes with an irregular dense central mass and a clear periphery. These different aspects represent different developmental stages, and indicate that maturation is rapid in this species. This was confirmed by the behavior of cysts placed on slides in a moist chamber. A considerable number, many of which had just formed, were so isolated on July 2, and all were found to have dehisced on July 4, no observation having been taken on July 3. The period is thus 1–2 days, which is in close agreement with that of *Gregarina achetæ-abbreviatæ*.

Dehiscence is by a single sporoduct, which may reach a length of 750 microns. A discharged cyst is shown in fig. 12. The residuum is a loose mass of granules and débris which nearly fills the cavity within. The duct is limited externally by a cuticular wall. Within it is filled by a soft substance, through the center of which can be seen the lumen along which the spores had passed. This lumen, however, shows no definitive membrane, being merely a channel through this soft substance, which is probably of the same nature as the residuum.

In one case observed, the spores still lay in situ as they had been projected from the duct. The duct was 600 microns long; the file of spores 2,400. Hence the leading spore had reached a distance of 3 millimeters from the cyst. In consideration, however, of the size and activity of the host, it is not easy to see how the scattering of the spores over such an infinitesimal area can cut much of a figure in their dissemination.

Spores.—Rounded cylinders or barrel-shaped. Dimensions, 5 by 2.75 microns.

Host.—Gryllus abbreviatus Serv. The gregarines occurred in perhaps 25 per cent. of the crickets opened. But when present, they are present in countless numbers, compact masses of gregarines as large as peas being found. It does not seem likely that such extensive infections can be due merely to the chance picking up of stray spores. More probably we have here to do either with cannibalism or the devouring of dead comrades.

Gregarina melanopli sp. n. (Pl. XVIII, figs. 6-9.)

Protomerite.—In the young solitary animals, the protomerite is cubical, with rounded corners, to mammaliform, and often shows in front a low, broad projection. In the associated gregarines, it has the form of a greatly compressed hemisphere.

Deutomerite.—In the young, cylindrical to flask-shaped. There is generally a slight constriction in the middle. In the pairs, cylindrical, but with a very variable ratio of length to breadth. Two cases are shown in figs. 8 and 9, which are camera outlines of living gregarines.

Epicyte.—Longitudinally striated. The following measurements of its thickness are taken from a large pair:

Primite.—

Anterior tip of protomerite					5 r	nicrons.
Sides of protomerite					5	"
Sides of deutomerite					1-2	"

Satellite.—

Anterior corners of protomerite				3	${f microns.}$
Sides of deutomerite				1-2	"
Posterior end of deutomerite				4	"

Sarcocyte.—Differentiated into an outer hyaline and an inner granular layer. Its thickness in the various parts of the same large pair from which the above measurements of the epicyte were taken is given in the following table:

Primite.—

Front of protomerite Sides of protomerite . Sides of deutomerite .								5	"
Satellite.—									
Anterior corners of prof Sides of deutomerite.	tom	erit	e .			٠	10	$^{16}_{-12}$	$\mathop{\mathrm{microns}}_{\mathcal{U}}.$
Posterior end of deuton									

It may be noted here that in those parts where the epicyte thickens, the sarcocyte thins. A like condition has been noted by Léger for *Amphoroides polydesmi*.

Entocyte.—Very dense. Tinged with brownish yellow. The nucleus shows merely as a lighter area.

Size.—The solitary animals ranged in length from 200–370 microns. The lengths of a number of pairs, in microns, are given in the appended list:

Primite.	Satellite.	Total.
675	750	1425
640	710	1350
600	750	1350
600	710	1310
600	700	1300
525	500	1025
420	450	870

The first was the largest pair seen. In nearly all cases, the primite was the shorter and broader animal.

Habit.—The gregarines, according to the particular host examined, were either nearly all solitary or nearly all associated. I examined, however, but very few locusts; so cannot say if this be the rule. In one, in which I found some fifty pairs, they occurred in an almost solid mass in the host's intestine, gradually separating when placed upon the slide.

Movements.—The animals are somewhat polymorphic, undergoing

fairly extensive changes of shape. Such changes, however, were always effected very slowly. They also progressed in curves and straight lines, but in a most leisurely manner.

Host.—Melanoplus femoratus (Burm.). Locality.—Wyncote, Pennsylvania.

As with his G. achetæ-abbreviatæ, so with his G. locustæ-carolinæ, Leidy (1853) seems to have described two species under one name. My observations of the summer of 1906 show that the host in question, Dissosteira carolina (L.), then known as Locusta carolina, is infected by two gregarines. One of these is in all probability a true Gregarina, and I believe Leidy's figs. 35 and 36 to be representations of it. On the other hand, his fig. 37 is probably a Stephanophora, and it has been placed in that genus by me (Crawley, 1903). The confusion seems best cleared up by retaining Leidy's name for the true Gregarina, and creating a new one for the Stephanophora. The two species are defined below.

Gregarina locustæ-carolinæ Leidy. (Pl. XVIII, fig. 13.)

Gregarina locustæ-carolinæ Leidy (1853), p. 239, pl. 11, figs. 35, 36. Gregarina locustæ-carolinæ Leidy (1856), p. 47. Gregarina fimbriata Diessing (1859), p. 730. Gregarina locustæ-carolinæ Labbé (1899), p. 35. Stephanophora locustæ-carolinæ Crawley (1903), p. 54.

Epimerite.—A small rounded knob, cut off from the protomerite by a very short neck. The epicyte of the epimerite is continuous with that of the protomerite, and does not intervene between the two segments, the boundary between which is formed by the sarcocyte of the protomerite. A small quantity of entocyte is present.

Protomerite.—Globular in the cephalonts, and nearly so in the sporonts. Posterior boundary plane.

Deutomerite.—Globular to oval or even cylindrical in the cephalonts. Oval to cylindrical in the sporonts.

Epicyte.—Shows a double contour.

Sarcocyte.—In the cephalonts and very small sporonts, well developed, especially in the anterior part of the protomerite.

Entocyte.—Pale. This applies to the young animals; my notes being silent as to its condition in the adults.

Nucleus.—Large, with one large karyosome.

Size.—The largest animal seen was 350 microns long. The appearance of this individual, however, did not suggest full maturity. The cephalonts were 100–110 microns long. Decapitation takes place early. Quite a number of small gregarines were seen, all about 100

microns long, the youthfulness of which was plainly indicated by their transparency, and fully half had lost their epimerites.

Host.—Dissosteira carolina (L.).

Locality.—Wyncote, Pennsylvania.

Stephanophora pachyderma sp. n. (Pl. XVIII, figs. 2, 3.)

Gregarina locustæ-carolinæ Leidy (1853), p. 239, pl. 11, figs. 37, 38. Gregarina locustæ-carolinæ Leidy (1856), p. 47. Gregarina fimbriata Diessing (1859), p. 730. Gregarina locustæ-carolinæ Labbé (1899), p. 35. Stephanophora locustæ-carolinæ Crawley (1903), p. 54.

Epimerite.—Consists of a cylindrical piece, bearing in front a number of forwardly directed digitiform processes. Separated from the protomerite by a mere constriction, no definitive neck being formed.

Protomerite.—In the cephalonts, consisting of a cylindrical basal portion, narrowing regularly in front to the base of the epimerite. This anterior conical part, which makes up one-half the length of the protomerite, is composed entirely of ectosarc. In the sporonts, almost perfectly hemispherical, with its contour continuous with that of the deutomerite.

Deutomerite.—In the cephalonts, lanceolate, with a blunt posterior Broader than the protomerite, and broadest just behind the septum. There is scarcely a constriction between the two. In the sporonts, heart-shaped.

Epicyte.—Thickness 2-3 microns. The thickness is essentially uniform over the entire gregarine, except for a small region at the anterior tip of the protomerite. Here the epicyte thickens on its inner surface, making a small indentation into the sarcocyte.

Sarcocyte.—Always very thick. In the cephalonts, making up onehalf the length of the protomerite. On account of the change of shape which follows decapitation, the sarcocyte is more conspicuous in the protomerite of the cephalonts than in that of the sporonts. Yet even in the latter, it here measures 30 microns, which is reduced to 12 microns elsewhere.

Entocyte.—In the sporonts, black in transmitted light in the deuto-Not quite so dense in the protomerite, and here showing a relatively clear space, as indicated in fig. 3.

Nucleus.—Fairly large, with a number of karyosomes.

Size.—The largest sporont seen was 500 microns long.

Host.—Dissosteira carolina (L.).

Locality.—Wyncote, Pennsylvania.

The perfectly oval shape of this last species, sometimes disguised by their habit of holding the long axis bent, is probably normal. one balloon-shaped specimen was seen.

The animals are present only sparingly in the infected locusts, and occur in both the mid-gut and pyloric cæca.

One specimen was observed which showed behind it a gelatinous stalk, such as described by Schewiakoff (1894), and considered by him to furnish the means for the progressive movement. This stalk, although differing but very slightly in refractive index from the water, could plainly be seen. Since, however, the stalk was carried about by the gregarine as a mammal carries its tail, the sole influence it could have possibly had upon progression would have been that of a hindrance.

The actual extrusion of the substance of this stalk was not witnessed, but that the gregarines were liberally provided with some kind of a gelatinous matter was demonstrated by killing them with iodine. Animals so killed showed, on their surfaces, great numbers of small globules.

I have finally to describe a *Geniorhynchus*, probably distinct from the European form.

Geniorhynchus æshnæ sp. n. (Pl. XVIII, fig. 4.)

Epimerite.—Consists of an ellipsoidal or globular head, borne on a short neck which may be considerably swollen. The head is liberally provided with short spines, directed backward.

Protomerite.—Large, having the form of a truncated cone with slightly curved contours. Broader than the deutomerite.

Deutomerite.—Conical to cylindrical, terminating bluntly. The posterior fourth generally showed, in the cases observed, one or more deep constrictions, which underwent slow changes.

Epicyte.—Thin, longitudinally striated.

Sarcocyte.—Well developed. In the protomerite, it is enormously thickened, occupying the anterior third of the segment as a solid mass, which rapidly thins out behind. It here contains a few small granules.

Entocyte.—Not especially dense, and usually thinning out considerably toward the surface.

Nucleus.—Shows several irregularly shaped karyosomes.

Size.—420 microns long.

Host.—Nymph of Æshna constricta Say.

Locality.—Southeastern Pennsylvania.

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EXPLANATION OF PLATE XVIII.

- Fig. 1.—Gregarina achetæ-abbreviatæ (p. 220). Camera outline of sporont.

 Fig. 2.—Stephanophora pachyderma (p. 226). Cephalont.

 Fig. 3.—Stephanophora pachyderma (p. 226). Sporont.

 Fig. 4.—Geniorhynchus æschnæ (p. 227). Cephalont.

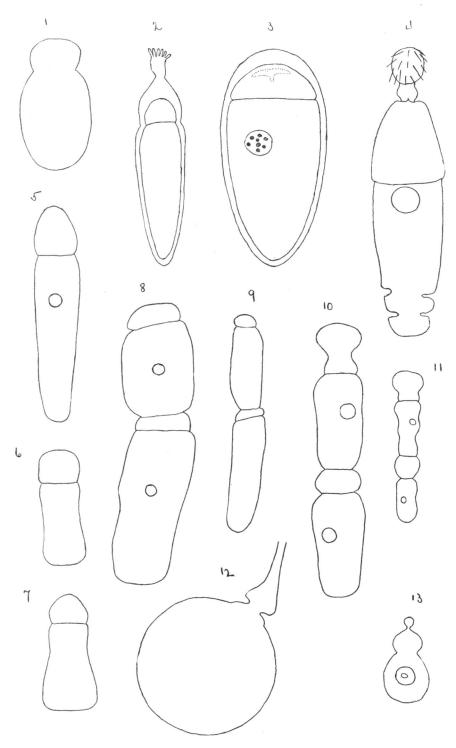
 Fig. 5.—Stenophora erratica (p. 221). Young sporont.

 Figs. 6, 7.—Gregarina melanopli (p. 223). Young solitary sporonts.

 Figs. 8, 9.—Gregarina melanopli (p. 223). Camera outlines of two pairs.

 Figs. 10, 11.—Gregarina kingi (p. 223). Paired individuals.

 Fig. 12.—Gregarina kingi (p. 221). Discharged cyst. Only the basal portion of the sporoduct is shown. the sporoduct is shown.
- Fig. 13.—Gregarina locustæ-carolina (p. 225). Cephalont



CRAWLEY ON GREGARINES